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INHERITANCE OF RESISTANCE IN OATS TO PUCCINIA GRAMINIS AVENAE

BY

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INHERITANCE OF RESISTANCE IN OATS TO PUCCINIA GRAMINIS AVENAE [1]

By S. M. Dietz [2]

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INTRODUCTION

The production of disease-resistant plants by hybridization has engaged the attention of biologists with increasing interest since 1878, when Darwin (*6*)[3] reported the production by James Torbitt of a fungus-proof potato. It was not until 20 years later, however, that Farrer (*10*) demonstrated the production of rust-resistant cereals. Varietal resistance, hybridization for the production of new resistant varieties, and the factorial analysis of the inheritance of resistance have been extensively studied during the last decade.

Henning (*15*), in Sweden, and later, Hungerford and Owens (*16*), in this country, have shown that there is a marked difference in the susceptibility of wheat varieties to *Puccinia glumarum* (Schm.) Erikss. and Henn. Hungerford and Owens, in greenhouse and field tests, showed many of the common wheats to be resistant. In 1920 Melchers and Parker (*20*) reported three Crimean hard winter wheats that were resistant to leaf rust, *P. triticina* Erikss.

Mains and Leighty (*18*), working with rye, an open-pollinated plant, found that 68 different selections were resistant to *Puccinia dispersa* Erikss.

The reaction of oat varieties to *Puccinia coronata* Corda and *P. graminis* Pers. has been studied by Parker (*23*). Of the 120 strains tested, 80 were susceptible to both rusts. White Tartar and Ruakura Rustproof proved resistant to *P. graminis*, while Burt and several others of the red-oat group (*Avena byzantina* C. Koch) were resistant to *P. coronata*. In 1920 Durrell and Parker (*8*) made a comprehensive survey, involving the assembling of data for five years, on the response of oat varieties to crown and stem rusts under field conditions. White Russian and Green Russian were found to possess a marked resistance to *P. graminis*. In a previous report (*7*) by the present writer, Richland (Iowa No. 105) was shown to be resistant to stem rust.

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[2] The writer wishes to express his thanks to I. E. Melhus, plant pathologist of the Iowa Agricultural Experiment Station, and to C. R. Ball and H. B. Humphrey, of the Office of Cereal Crops and Diseases, for suggestions and criticisms during the progress of the work and the preparation of the manuscript; also to the many assistants who ably aided in the collection of the data presented.

[3] Reference is made by number (italic) to "Literature cited," p. 22.

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Although the varietal response to the rusts is known, it often is necessary to produce new varieties by hybridization. Biffen (*3, 4, 5*) found susceptibility to *Puccinia glumarum* dominant and secured a monohybrid segregation in the F_2 generation. On the other hand, Nilsson-Ehle (*22*) concluded that distinct dominance of susceptibility to this rust was of rare occurrence. Hayes, Parker, and Kurtzweil (*14*), in their investigation of varietal resistance of wheat to *P. graminis tritici* Erikss. and Henn., found the F_2 and F_3 generations segregating for resistance and susceptibility, although sterility probably prevented an expression of the true ratios. Parker (*24*) showed that resistance to *P. coronata* was heritable and suggested a multiple factor explanation. In 1922, Garber (*11*) found resistance in oats to stem rust, *P. graminis avenae* Erikss. and Henn., to be dominant and due to a single-factor difference in Minota-White Russian and Victory-White Russian crosses.

Stakman and Levine (*26*), Melchers and Parker (*19*), and others have shown the existence of 37 physiologic forms of rust within *Puccinia graminis tritici*, and Stakman, Levine, and Bailey (*27*) later isolated four such forms within *P. graminis avenae*. Because these specialized forms exist, it is imperative to determine the response of wheat and oat varieties to each of them. Puttick (*25*), Aamodt (*1*), Harrington and Aamodt (*12*), and Hayes and Aamodt (*13*) have studied the reaction of wheat hybrids to many of these forms.

The possible existence of linkage between rust resistance and other characters has been shown by Hayes, Parker, and Kurtzweil (*14*) and by Waldron (*28*) in wheat, and by Garber (*11*) in oats. In none of these cases was the linkage sufficiently close, however, to prevent the production of varieties which were rust resistant and endowed with other desirable characters.

The manner of inheritance of rust resistance in wheat has been demonstrated by Hayes, Parker, and Kurtzweil (*14*) to be different for a durum-common and an emmer-common cross. Whether such a difference can be obtained in oat species and varieties has not previously been known. It is the purpose of this paper to report the manner of inheritance of resistance to *Puccinia graminis avenae* by eight varieties of oats belonging either to *Avena sativa* L. or *A. byzantina* C. Koch.

METHODS AND MATERIALS

Preceding a consideration of the inheritance of rust resistance in oats, adaptations of existing methods and the development of many new ones were necessary. The fact that many data were taken on each individual plant necessitated detailed planting, harvesting, and recording methods, together with special means of producing an epidemic of the rust and estimating its subsequent effect on these plants.

SOURCE OF OAT VARIETIES

The eight pure-line varieties of oats used as parent material of the hybrids treated in this study are described below.

The strain of Burt was a head selection from C. I. No. 710 [4] in 1916. It is a reddish black oat belonging to the species *Avena byzantina* and is susceptible to *Puccinia graminis avenae* but moderately resistant to *P. coronata*.

[4] Cereal Investigations accession number.

The Early Ripe variety was a head selection from the material obtained by J. H. Parker, formerly of the United States Department of Agriculture, from H. H. Love, of Cornell University, Ithaca, N. Y. It is similar to Burt except that it has a finer straw and usually a lighter colored grain. It has fewer basal hairs and a less pronounced cavity at the base of the first floret. It is susceptible to both oat rusts.

The Green Russian variety was a selection from Minnesota No. 350 and belongs to the species *Avena sativa*. It is resistant to stem rust and moderately resistant to crown rust.

The Richland (Iowa No. 105) variety is a yellow selection from Kherson produced by L. C. Burnett, of the Iowa Agricultural Experiment Station, in cooperation with the United States Department of Agriculture. The material used here was a head selection from this pure line. It is an extremely early oat, an excellent yielder, and resistant to *Puccinia graminis avenae*. It often escapes *P. coronata* under field conditions in Iowa because of its early maturity.

The Lincoln variety was obtained from H. H. Love, of Cornell University. It is similar to Swedish Select, except that two-kerneled spikelets predominate. It yields well in the cooler sections of the United States, especially New York, but is susceptible to stem rust.

National, a variety similar to Silvermine, also was obtained from Cornell University. It is a good yielder, of mid-season maturity, but susceptible both to *Puccinia graminis avenae* and *P. coronata*.

The Ruakura variety was obtained from a head selection made in 1916 from C. I. No. 701. It is a slender-stemmed, early-maturing oat belonging to the species *Avena byzantina*. Ruakura is similar to Burt in vegetative growth, but has pubescent nodes. It possesses a moderate degree of resistance to both oat rusts.

According to Etheridge (*9*), the White Russian and White Tartar varieties are indistinguishable. White Russian was a head selection from Minnesota No. 5, whereas White Tartar was obtained from Cornell University. Both of these are side-panicled, late-maturing, low-yielding strains, belonging to *Avena sativa* var. *orientalis*. They possess marked resistance to *Puccinia graminis avenae*.

SOWING

The seeds were sown in 10-foot rows spaced 1 foot apart. In 1920, the individual seeds were spaced 6 inches apart in the row, but this distance was reduced to 4 inches in all the subsequent years of the experiment. In both the F_1 and F_2 sowings, only the primary kernel was used, the second floret or "pin" oat having been removed. This method permitted only one plant to emerge in a single space, thereby removing the difficulty of separating heavily tillered plants.

The F_1 seeds were divided into three lots. The first portion was sown in 1920 and produced the F_2 generation. F_2 plants were grown from the second portion in 1921 adjacent to the F_3 generation and compared with it. The third portion, with a similar remnant of F_2 seed and some of the original crossed seed, was sown in 1922, so that the F_1, F_2, and F_3 generations were grown side by side in that year.

Two series of control rows were necessary. Every tenth row was sown to the same susceptible pure-line variety to gauge the uniformity of the epidemic produced in the nursery, and the resistant or susceptible pure-line parents were sown every twenty-fourth and twenty-

fifth row, respectively, in order to compare their rust response with that of their progeny. The culture of the nursery was uniform.

RECORDING

Each cross was given a number. For instance, White Russian×Burt was given number 274, which was used for all subsequent generations. Each F_1 plant of this cross or its reciprocal was given a subnumber; that is, 274–1, 274–2, 274–3, etc. Reciprocal crosses were made and their progeny studied to determine the differential influence, if any, on the progeny. No differences were noted, however, and in order to simplify the presentation of the data a cross and its reciprocal are considered as a single cross.

Each plant was given a position number. This method allowed for comparison of the response of each individual plant with each adjoining plant in the office records as well as under field conditions. The following data were taken on each plant: Dates of seeding, heading, maturing, and harvesting; percentage of rust infection; size of uredinia; height; shape of panicle; and yield.

HARVESTING

All of the individuals of the F_1 and F_2 generations were harvested separately. The panicles of each plant were wrapped in a separate paper and the product of the entire row was inserted in a paper bag. Each F_3 plant was labeled with a string tag, and the plants in the entire row were bagged together but threshed as individual plants.

TECHNIC OF PRODUCING EPIDEMICS

The classification of the individual plants into either the resistant or the susceptible group depended upon their relative response to inoculation by *Puccinia graminis avenae*. Theoretically, this classification was based upon the fact that all plants had equal opportunity for maximum infection. In order to afford this opportunity, the following methods of exposing the plants were used:

(1) Oat plants infected with stem rust were transplanted directly into the nursery from the greenhouse. These plants had been infected with urediniospores collected from the nursery in the previous year and maintained in greenhouse stock cultures.

(2) Urediniospores were scraped from oat plants in the greenhouse, placed in distilled water, and sprayed on the culms with an atomizer.

(3) Urediniospores were scraped from oat plants in the greenhouse and dusted on the previously moistened oat plants in the field.

(4) Urediniospores were applied directly to the leaves of the oat plants by means of a scalpel between 7 and 8 o'clock p. m. The plants thus exposed were covered with a bell jar for 12 hours.

In 1919 and 1920 plants in the field were exposed to infection when 6 to 9 inches high. It was noted, however, that very few became visibly infected until the panicles had just emerged from the sheath. From 1921 to 1923, therefore, the plants were not exposed until this stage of maturity was reached.

CLASSIFYING PLANTS BY SIZE OF UREDINIA

Each individual plant was classed as resistant or susceptible by using the scale devised by N. A. Cobb in Australia and later revised and used by the Office of Cereal Crops and Diseases, United States

Department of Agriculture.[5] This scale is based on the proportion of the total area covered by uredinia, no consideration being given to the relative size of the sori, though it will be shown later that the size of the rust sorus can be correlated directly with resistance. In addition to the quantitative estimate of rust, the size of uredinia is used in this paper in classifying the response of the individual plants to rust.

Rust estimates were started on the standing plants about three weeks before harvest and continued until harvest. During the last week of this period the plants were harvested and estimated at the same time. Only one rust estimate was made for each plant. The whole plant was inspected and the maximum infection accepted as indicating its degree of resistance. It was not uncommon to find certain culms of a single plant more heavily infected than others. Uredinia and telia were estimated collectively during the last few days of each season, for the fungus rapidly enters the telial stage as the oat plant matures. Progenies of all plants which could not be classified as either susceptible or resistant under field conditions were tested in the greenhouse or in the field the following spring.

As noted above, the size of the uredinia was employed as a measure of susceptibility. (Fig. 1.) During the progress of this work the resistant pure-line varieties of oats developed a consistently low percentage of infection. Many of the susceptible varieties varied in reaction from apparent resistance to susceptibility. These results could be explained in one of two ways: (1) The pure-line varieties of oats were not homozygous for susceptibility to rust; or (2) they were homozygous and certain plants were escaping infection or at least severe infection. It then became necessary to find some other index by means of which these escaping plants might be classified according to their inherent response to rust. Such an index was found in the size of uredinia.

If, then, the size of uredinia can form the basis for differentiating susceptible and resistant plants, how are small and large uredinia to be distinguished? Although these two classes were only relative, they none the less were sharply defined. Hence the classification was reasonably accurate because the greater dimension of the large uredinia was more than ten times that of those classified as small.

Pure-line resistant varieties of oats, under field conditions, consistently showed a low percentage of infection and small-sized uredinia. Pure-line susceptible varieties differed greatly in percentage of infection, but uniformly produced large uredinia. In progeny tests of 100 individuals, having a low percentage of infection but large uredinia under field conditions, 1,649 plants were produced the next year with a high percentage of infection and large uredinia. Clearly, then, these plants had partially escaped stem rust the first year but could have been classified as susceptible on the basis of size of uredinia.

Although pure lines showed a positive correlation between size of uredinia and response of the host to rust, it was not known whether hybrids acted in the same way. In addition to the data on size of uredinia on F_1 plants recorded in Table 1, records of F_2 and F_3 plants of Green Russian × Richland and White Russian × Burt, and F_4

[5] Scale for estimating rust. In Cereal disease field notebook. U. S. Dept. Agr., Bur. Plant Indus., Cereal Invest., C. I. form 11. [June, 1915.]

plants of White Tartar × National and White Tartar × Lincoln were made. The susceptible F_1 plants, subsequently classified as susceptible by the reaction of both the F_2 and F_3 progeny, had large uredinia. An F_3 progeny test includes the F_3 individuals from a single F_2 plant. The F_1 individuals classified in Table 1 as resistant, and subsequently proving to be so, had small uredinia. In the total F_2 population in all years, 10,004 plants were classified as resistant and had small

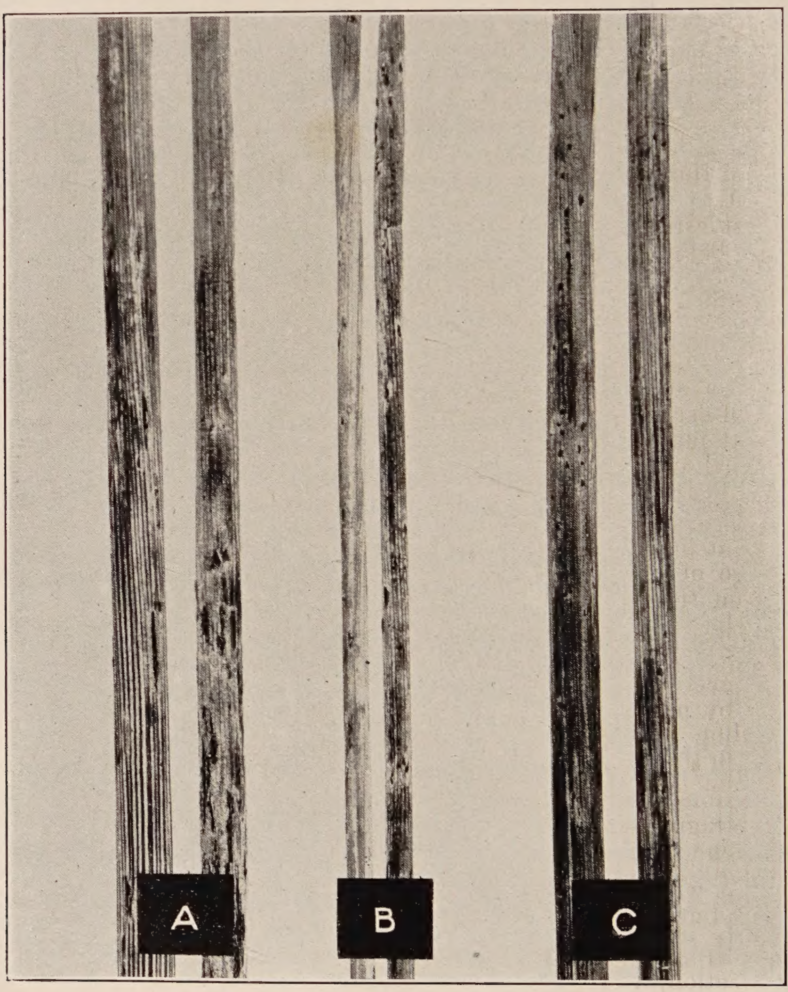

Fig. 1.—Size of urediniosori in an F_3 progeny of White Tartar × Lincoln: A, Large urediniosori (susceptible plant); B, intermediate urediniosori (susceptible plant); and C, small urediniosori (resistant)

uredinia, while 713 were susceptible, with large uredinia. In the test of the F_3 progeny, those rows segregating for rust reaction also segregated for size of uredinia, the individual susceptible plants having large uredinia.

Among the 2,700 F_2 plants studied for size of uredinia in 1920, all those placed in the large-uredinia group showed susceptibility in further progeny tests.

TABLE 1.—*Reaction of F_1 plants to Puccinia graminis avenae, showing correlation between size of uredinia and rust susceptibility*

Cross	Hybrid No.	Number of seeds set	F_1 reaction to P. graminis avenae (number of plants)			
			Resistant		Susceptible	
			Size of uredinia		Size of uredinia	
			Large	Small	Large	Small
White Russian×Burt	274	27	0	15	12	0
Green Russian×Burt	283	10	0	2	8	0
Siberian×Burt	1206	6	0	0	6	0
White Russian×Ruakura	271	2	0	0	2	0
Green Russian×Early Ripe	280	2	0	2	0	0
Green Russian×Richland	277	5	0	5	0	0
Total		52	0	24	28	0

It should be pointed out that not all plants having small uredinia are resistant, but that any of these plants, grown under field conditions, could be classed as susceptible if large uredinia were present on the culms, regardless of the percentage of infection.

Time of maturity perhaps is one of the chief causes for lack of perfect correlation between size of uredinia and resistance. All of the 100 rust-escaping plants mentioned above were mature from 7 to 10 days earlier than their susceptible sisters. It is probable, then, that maturity, accompanied by senility of the host cells, prevented further development of this obligate parasite. This conclusion is supported by the fact that many of the susceptible early-maturing plants had both large and small uredinia, indicating that the uredinia develop but little after the maturity of the host. Progeny from these plants, when infected at an earlier stage in the next year, were susceptible and produced only large uredinia.

The correlation of size of uredinia and rust reaction under greenhouse conditions is not so marked as in the field. As all stem-rust inoculations were made on the leaf blades in the greenhouse and on the culms in the field, some difference would be expected. Type of infection indicated by hypersensitive areas assisted in differentiating the oat plants grown in the greenhouse into either resistant or susceptible groups.

HYBRIDIZING IN THE GENUS AVENA

Before the production of oat hybrids was begun in 1919, a survey of the literature was made, but this revealed little information on the technic of crossing oat varieties under field conditions. Although field crossing can be done very successfully in some sections of the United States, in other sections successful crosses are obtained with difficulty owing probably to such factors as temperature and humidity. In the opinion of the writer, field crossing should be practiced only when greenhouse facilities are not available, as oats sown in the greenhouse in November, and heading in March, permit a high percentage of successful crosses. A consideration of such problems as length of time between emasculation and pollination, time of day best suited for

pollinating, and quantity of pollen necessarily precedes the successful production of oat hybrids.

PERIOD BETWEEN EMASCULATION AND POLLINATION

In making an oat cross, the anthers must be removed from the inclosing lemma and palea before the pollen is shed on the stigmatic surface. It would be more convenient to remove the anthers and immediately insert the foreign pollen. Using White Russian as the female parent and Burt as the male, pollinations were made at the time of emasculation and at the end of each succeeding 12-hour interval up to 72 hours under field conditions. The first series, consisting of 10 pollinations on each of two panicles, was made at 7.30 o'clock a. m., the next at 7.30 o'clock p. m. The general method of pollination for all hybrids reported below involved cutting all except 10 spikelets from the panicle of the female parent on emergence from the sheath. The second floret was removed from each of these spikelets and the remaining primary florets were emasculated. An oil-paper bag was then placed over each prepared panicle and tied at the base with a string.

The results showed about the same percentage of seeds produced from pollinations at each of these periods. However, in testing these seeds, the F_1 plants indicated that 6 out of 20 of the resulting seeds were self-fertilized when emasculation and pollination occurred at the same time. A higher percentage of hybrids was produced when pollination occurred 48 hours after emasculation.

EFFECT OF TIME OF DAY ON SEED SETTING

Using the White Russian × Burt cross, the influence of time of day on set of seed was determined under field conditions. Pollinations were made at Ames, Iowa, and Iron River, Wis., at intervals from 4.30 o'clock a. m. until 8.30 o'clock p. m. on three consecutive days at each place.

At these two places 770 pollinations were made on 77 different panicles. The results are presented in Table 2. From these pollinations 78 seeds resulted, an average of 10.1 per cent for the entire experiment. From the forenoon pollinations 36 seeds were obtained and 42 from those made in the afternoon. During the six days no seed was set from pollinations made between 11.30 a. m. and 2.30 p. m. The failure to set seed on June 28 at Ames is difficult to explain, as the mean temperature and general characteristics were similar on these three days except for low relative humidity on June 28.

At Ames, out of a total of 180 pollinations made in the forenoon 17 were successful, as compared with 9 from a total of 210 pollinations made in the afternoon. At Ames no seed was set from pollinations made between 10.30 a. m. and 3.30 p. m.

At Iron River, Wis., 19 out of a total of 180 attempts were successful in the morning and 33 from a total of 210 in the afternoon. The interval during which no seeds were set was about two hours shorter at Iron River than at Ames. It is probable that such factors as temperature and relative humidity influence the effectiveness of pollination at some hours of the day.

TABLE 2.—*Influence of time of day on effectiveness of cross-pollinating White Russian and Burt oat varieties under field conditions*

Place and date in 1919	Number of seeds resulting from cross-pollination at time of day indicated												
	Forenoon						Afternoon						
	4.30	5.30	8.30	9.30	10.30	11.30	12.30	2.30	3.30	4.30	5.30	7.30	8.30
Ames, Iowa:													
June 26	4	2	1	2	0	0	0	0	0	0	1	1	------
June 27	2	2	4	0	0	0	0	0	0	2	1	3	1
June 28	0	0	0	0	0	0	0	0	0	0	0	0	0
Iron River, Wis.:													
July 29	2	3	1	0	0	0	0	0	0	1	1	1	2
July 30	1	1	1	0	0	0	0	0	0	3	2	2	3
July 31	2	1	1	3	3	0	0	0	4	3	4	3	4
Total	11	9	8	5	3	0	0	0	4	9	9	10	10

QUANTITY OF POLLEN

Although Jelinek (*17*) draws no conclusions concerning the quantity of pollen necessary to fecundation, this may be a factor in the explanation of his results in the production of wheat hybrids by the following methods: (1) Insertion of a whole anther in the female floret, and (2) emasculation of spikes and bagging them together with spikes of similar maturity belonging to the pollen parent. He states that in 1916 the second method resulted in twice as much seed production as the first. In the unfavorable year of 1917 no seed was produced by the first method, whereas 50 per cent of the florets on 24 out of 47 spikes produced seed by the second method.

An easy method of pollination is to insert a whole anther from the male parent between the palea and lemma of a floret of the female parent. However, when using this method in studies here recorded, fewer seeds developed than when a small quantity of pollen was dusted on the stigmatic surface, even though all pollinations were made early in the morning and at least 24 hours after emasculation. Upon examining the florets of crosses made by inserting the whole anther between the lemma and palea, many molds were found growing abundantly on the surface of the caryopsis. The excess pollen probably served as a favorable medium for these molds and their action often prevented the formation of viable seed.

PHYSIOLOGIC FORMS OF RUST IN THE NURSERY

According to Stakman, Levine, and Bailey (*27*), four distinct physiologic forms of stem rust occur on oats, varying widely in their varietal reaction. Only two of these were found in America. As certain varieties of oats are resistant to one form and susceptible to another, it is imperative in any study of inheritance of rust resistance that the class of reaction to the fungus be known. The results obtained by Stakman and his associates naturally raise the question as to what form was prevalent in the nursery from year to year. Unfortunately, the geographic range of the physiologic forms found in America has not yet been determined. As no effective method, other than the one employed, has been devised to prevent physiologic forms from infecting oat hybrids grown under field conditions, it was

necessary to determine which form or forms were present each year. Four methods were used to accomplish this.

In the fall of 1919, a composite sample of *Puccinia graminis avenae* was taken to the greenhouse and maintained in stock culture in the urediniospore stage (*21*). This culture of rust was used to start the initial field infection in the spring of 1920. In the fall a composite sample of rust again was taken from the nursery and used as inoculum on nine pure-line parents. If these parents responded in the same manner to the 1919 and 1920 cultures, the 1919 culture was discarded and the later culture used in the field the next spring. This process was continued throughout the study.

As an additional test for the physiologic response of *Puccinia graminis avenae*, 100 pure-line varieties of oats were grown adjoining the oat-breeding nursery each year, every tenth row being the same pure-line control. These indicated the uniformity of the epidemic.

As already described, the initial infection was started each spring in this nursery with the same culture of *Puccinia graminis avenae* that had been overwintered in the greenhouse. During this five-year period, all varieties showing resistance in 1919 were resistant in the following four years and those susceptible in 1919 were uniformly susceptible thereafter. Moreover, each pure-line parent sown in the breeding nursery showed similar results each year from 1919 to 1923. The results thus far indicate either that only one physiologic form was present in the nursery during the entire time or that these pure lines did not act as differential hosts.

To identify the physiologic form employed in this investigation, the differential hosts of Stakman, Levine, and Bailey (*27*) were exposed to infection. A composite sample of stem rust from the oat-breeding nursery was taken to the greenhouse in July, 1923, and White Tartar, Monarch (C. I. 1760), and the awnless Monarch Selection of Etheridge (C. I. 1879) were inoculated. Monarch Selection of Etheridge (C. I. 1879) was susceptible and White Tartar resistant. According to Stakman and others (*27*), Monarch Selection (C. I. 1879) reacts as a differential host for forms 1 and 2, being resistant to the former and susceptible to the latter. These results suggest that only form 2 (*27*) was present, as Monarch Selection bore only one type of infection, which was normal, with numerous large, coalesced uredinia.[6]

HYBRID VIGOR OF F_1 PLANTS

In crossing certain varieties of oats, remarkable hybrid vigor, expressed as yield and height, was shown by the F_1 plants. (Fig. 2.) Some of these F_1 plants produced more than 2,200 seeds and varied in yield from 10.5 to 36 gm. The parents of these crosses were grown in the same year in field rows adjacent to the F_1 hybrids, but were greatly inferior in yielding capacity. In another cross, Richland (Iowa No. 105), the highest yielding parent, produced only about one-fifth as much as the lowest yielding hybrid of which it and Green Russian were the parents. It should be mentioned that oats make excellent material for genetic studies, as sufficient numbers can be readily obtained in the F_1 generation to make an F_2 inheritance study significant.

[6] Since the completion of these investigations, it has been shown by Bailey (*2*) that only certain selections of Monarch Selection of Etheridge act as differential hosts for physiologic forms 1 and 2 of *Puccinia graminis avenae.*

The yield in grams and the height in centimeters are the averages of at least 20 parental plants grown under the same cultural conditions as the hybrids. As shown in Table 3, the height in the F_1 did not

FIG. 2.—Hybrid vigor expressed in height in a White Russian × Burt cross. A, Burt parent; B, F_1 plant; C, F_2 plant; D, White Russian parent

increase in proportion to the yield, but usually was intermediate between that of the parents. Reciprocal crosses had a response similar to those reported in Table 3.

TABLE 3.—*Vigor of parent and F_1 plants of oats in 1919, as expressed by yield and height*

Parents and hybrids	Hybrid No.	Number of plants	Average yield (grams)	Average height (cm.)
White Russian		20	2.7	98
Ruakura		20	1.5	63
White Russian×Ruakura	271	2	22.5	89
Burt		20	2.1	70
White Russian		20	2.7	98
White Russian×Burt	274	4	14.1	90
Richland		20	3.8	79
Green Russian		20	2.6	97
Green Russian×Richland	277	5	21.5	100
Early Ripe		20	1.4	70
Green Russian		20	2.6	97
Green Russian×Early Ripe	280	2	27.5	94
Burt		20	2.1	70
Green Russian		20	2.6	97
Green Russian×Burt	283	3	19.7	91

FACTORIAL EXPLANATION OF RUST RESISTANCE IN OATS

Although rust resistance of cereals has been known to be a heritable character since 1898, when Farrer (*10*) produced resistant wheats by hybridization, the manner of inheritance was not clearly understood until lately. In order to predict the results of a cross between resistant and susceptible oat varieties, the manner of inheritance must be determined. A study of the segregation of the F_2 into resistant or susceptible plants, as verified by the behavior in the F_3, affords the basis for a factorial explanation. An attempt is made to explain the following crosses on a factorial basis.

CROSSES OF RESISTANT AND SUSCEPTIBLE VARIETIES

The first step in the usual method of obtaining material for a factorial explanation of the inheritance of any character involves crossing two individuals differing sharply with respect to this character. After determining the relative reaction of oat varieties to *Puccinia graminis avenae*, crosses were made between resistant and susceptible varieties. Obviously, more can be learned by making the other possible crosses, namely, resistant on resistant and susceptible on susceptible varieties. In this study, hybrids were produced only by crossing resistant with susceptible and resistant with resistant varieties.

RUST REACTION OF THE F_2 PLANTS

If resistance to rust is dominant, all individuals in the F_1 of the cross between resistant and susceptible varieties should be resistant. However, in the present experiments both resistant and susceptible F_1 plants were obtained from crosses involving the susceptible Burt and certain resistant varieties. As it has been shown that all of the 1,115 Burt plants examined were susceptible, this variety must be homozygous for susceptibility to stem rust.

In hybrids obtained from Green Russian×Early Ripe (hybrid No. 280–1 in Table 4), the F_1 was resistant and the F_2 segregated into 254 resistant and 64 susceptible plants. This approximates a 3:1 ratio. In a reciprocal cross (280–2) involving the same parents, the F_2 segregated into 250 resistant to 102 susceptible plants, again approaching a 3:1 ratio. Resistance is dominant and the cross can be explained by the assumption of a single-factor difference. Green

Russian could be symbolized as *SS* (resistant) and Early Ripe as *ss* (susceptible). The F_1, being *Ss*, would be resistant, and the F_2 would segregate in the proportion of 1*SS* : 2*Ss* : 1*ss*, or a 3:1 ratio.

TABLE 4.—*Rust reaction of F_1 and F_2 plants from crosses between resistant and susceptible varieties*

Cross	Hybrid No.	F_1		F_2		Ratio		Probable error	$\frac{D}{PE}$
		Resistant (S)	Susceptible (s)	Resistant (S)	Susceptible (s)	Calculated	S:s		
Green Russian×Early Ripe	280–1	S		254	64	238. 5:79. 5	3:1	±5. 21	2. 97
Early Ripe×Green Russian	280–2	S		250	102	264:88	3:1	±5. 48	2. 55
Green Russian×Burt	283–2		s	30	111	26. 4:114. 6	3:13	±3. 13	1. 15
Do	283–3	S		179	54	174. 8:58. 2	3:1	±4. 46	. 94
White Russian×Burt	274–4		s	23	77	25:75	1:3	±2. 92	. 68
Do	274–5	S		185	45	174:56	3:1	±4. 43	2. 48
Do	274–6		s	58	251	57. 9:251. 1	3:13	±4. 63	. 02
Do	274–8	S		26	8	25. 5:8. 5	3:1	±1. 70	. 29

White Russian×Burt (hybrid No. 274–6, Table 4) was susceptible in the F_1 and in the F_2 segregated into 58 resistant and 251 susceptible plants, thus closely approximating a 3:13 ratio. This cross may be explained on the basis of a two-factor difference, one of which was a resistance inhibitor.

The genotypic composition of the Burt parent in this case can be considered as *ssII*, when *s* = susceptibility and *I* = a resistance inhibitor. The genotype of White Russian, the resistant parent, would be *SSii* where *S* = resistance and *i* = absence of resistance inhibitor. With such an assumption, the F_1 would be *SsIi* or susceptible. The F_2 would segregate in the ratio of 3 resistant to 13 susceptible plants.

The actual results gave a close approximation to the theoretical, *PE* being ±4.63 and $\frac{D}{PE}$ equaling 0.02.[7] The F_3 results from this cross will be considered in detail in Table 5.

It is apparent from the above hypothesis that three genetically different strains of Burt might be obtained, each of which would breed true for susceptibility and maintain the three genetic compositions, namely, *SSII*, *ssII*, and *ssii*. The fact that these three different genotypes do exist, and breed true for susceptibility in what was thought to be a pure line of Burt, will be shown later. Hybrid No. 274–4, White Russian×Burt (Table 4), was susceptible in the F_1 and segregated into 23 resistant to 77 susceptible plants in the F_2. Fitting this cross to a 1:3 ratio resulted in a *PE* of ±2.92 and $\frac{D}{PE}$ of 0.68. The actual and the theoretical results do not entirely agree, but the deviation probably is not significant. This cross thus can be explained by assuming *SSii* as the genetic composition of White Russian and *SSII* as that of Burt.

In two other crosses of White Russian×Burt (hybrid Nos. 274–5 and 274–8, Table 4), the F_1 plants were resistant. No. 274–5 segregated into 185 resistant and 45 susceptible plants in the F_2. This approximates a 3:1 ratio, the *PE* of which was ±4.43 and $\frac{D}{PE}$

[7] *PE* = probable error; $\frac{D}{PE} = \frac{\text{deviation}}{\text{probable error}}$.

equaled 2.48. The F_2 of No. 274–8 segregated into 26 resistant and 8 susceptible plants. Assuming a 3:1 ratio, the PE was ± 1.70 and the $\frac{D}{PE}$ 0.29. Both of these could then be satisfactorily explained by assuming *SSii* as the factorial composition of White Russian and *ssii* as that of Burt.

The F_1 derived from a Green Russian × Burt cross was resistant (hybrid No. 283–3, Table 4). The F_2 contained 179 resistant and 54 susceptible plants. Explaining this cross on the basis of a 3 : 1 ratio, the PE was ± 4.46 and the $\frac{D}{PE}$ 0.94. Another F_1 plant (hybrid No. 283–2) was susceptible, and the F_2 segregated in the ratio of 30 susceptible to 111 resistant plants. Interpreting this result as representing a 3 : 13 ratio, the PE was ± 3.13 and the $\frac{D}{PE}$ was 1.15. Green Russian could then be represented as *SSii* and Burt as *ssii*.

It should be pointed out here that Green Russian and White Russian crosses can be explained by assuming the same genetic composition for both of these pure-line parents, while Burt, which breeds true for susceptibility to rust, has at least three different genetic compositions which breed true for susceptibility.

Rust Reaction of the F_3 and F_4 Plants

WHITE RUSSIAN×BURT

As shown in Table 4, one cross of White Russian × Burt (hybrid No. 274–6) was susceptible to *Puccinia graminis avenae* in the F_1 generation. The segregation following this cross differed from that of many other crosses made both by Garber (*11*) and by the writer in that the F_2 generation contained 3 resistant to 13 susceptible plants. These F_2 resistant plants showed, on an average, in the F_3 progeny test that one bred true for resistance, while two progenies split in the ratio of 3 resistant to 1 susceptible plant. (Fig. 3.)

Placing these results on a factorial basis, the following factors were assumed: S = resistance, s = susceptibility, I = resistance inhibitor, i = absence of inhibitor.

White Russian, then, might be represented as *SSii* and Burt as *ssII*. The following outline would then represent the reaction of the parents and the F_1, F_2, and F_3 generations:

White Russian *SSii* (resistant) × Burt *ssII* (susceptible)

F_1 reaction	F_2 individual plant reaction	F_3 progeny tests
SsIi susceptible.	1 *SSII* susceptible	Homozygous susceptible.
	2 *SSIi* susceptible	1 resistant, 3 susceptible.
	2 *SsII* susceptible	Homozygous susceptible.
	4 *SsIi* susceptible	3 resistant, 13 susceptible.
	1 *SSii* resistant	Homozygous resistant.
	2 *Ssii* resistant	3 resistant, 1 susceptible.
	1 *ssII* susceptible	Homozygous susceptible.
	2 *ssIi* susceptible	Do.
	1 *ssii* susceptible	Do.
	16	

This hypothesis allows a satisfactory explanation of the actual results obtained in this cross of White Russian × Burt (hybrid No. 274–6) as shown in Table 5.

It is well to point out in this connection that the criterion of the whole behavior in this cross is the susceptibility of the F_1 and the two

FIG. 3.—Culms from two F_3 plants of a White Russian×Burt cross. These two plants grew side by side in the same nursery row: A, susceptible; B, resistant

genetically distinct resistant F_2 hybrids, produced in the proportion of one which breeds true for resistance to two which are heterozygous and segregate into three resistant plants to one susceptible plant. A summary of the breeding behavior in the F_3 is presented in Table 5.

TABLE 5.—*Breeding behavior for rust reaction of F_3 families of oats grown from seed of individual F_2 plants of crosses between White Russian and Burt (274–6)*

Breeding behavior in the F_2	Breeding behavior in the F_3: Number of homozygous resistant		Number of heterozygous with ratio of— 3:1			1:3 and 3:13			Number of homozygous susceptible	
	Families	Plants	Families	Plants: Resistant	Plants: Susceptible	Families	Plants: Resistant	Plants: Susceptible	Families	Plants
58 resistant: Observed	19.0	348	39.0	723	229	-------	-------	-------	-------	-------
58 resistant: Calculated	19.3	348	38.7	714	238	-------	-------	-------	-------	-------
58 resistant: Deviation	.3	-------	.3	9	9	-------	-------	-------	-------	-------
251 susceptible: Observed	-------	-------	-------	-------	-------	111.0	748	2,869	140.0	4,755
251 susceptible: Calculated	-------	-------	-------	-------	-------	115.9	753	2,864	135.1	4,755
251 susceptible: Deviation	-------	-------	-------	-------	-------	4.9	5	5	4.9	-------

The 58 resistant F_2 plants produced 19 F_3 families homozygous for resistance where the expectation was 19.3, and 39 heterozygous where the expectation was 38.7. These latter segregated in the ratio of three resistant to one susceptible plant. The deviation of 0.3 needs no further consideration. The 251 susceptible F_2 plants produced 140 F_3 families homozygous for susceptibility and 111 heterozygous where the expectation was 135.1:115.9. Insufficient plants of the F_3 families were grown to differentiate the 3:13 and 1:3 ratios, respectively.

WHITE TARTAR×NATIONAL

Through the kindness of H. H. Love, of Cornell University, 86 F_2 plants of White Tartar × National (278a) were sent to the writer at Ames, Iowa, in the spring of 1921. Seed from part of these plants was sown that spring and seed from the remaining part in 1923. The National variety is extremely susceptible to stem rust, and White Tartar is resistant. (Fig. 4.) The F_1 and F_2 generations of this cross had been grown at Ithaca, N. Y., where their reactions to stem rust were not recorded. From these 86 F_2 plants, 2,100 F_3 individuals were produced. Of these F_3 families 20 bred true for resistance, 19 bred true for susceptibility, and 47 segregated, producing 854 resistant to 303 susceptible plants. The data for both 1921 and 1923 are summarized in Table 6.

Placing this cross on a factorial basis, White Tartar could be expressed as *SSii* and National as *ssii*. A ratio of 3 resistant to 1 susceptible would be expected in the F_2. In the F_3, 1 F_2 plant should breed true for resistance, 2 should segregate in a ratio of 3 resistant plants to 1 susceptible plant, and 1 should breed true for susceptibility. Explaining this cross on a 3 : 1 ratio, it is found that the resistant F_2 had a PE of ± 2.70 and the $\frac{D}{PE}$ was 0.9. The 47 heterozygous progenies splitting into 854 resistant to 303 susceptible plants had a PE of ± 9.93 and the $\frac{D}{PE}$ was 1.38.

FIG. 4.—Characteristic appearance of susceptible and resistant parents in an oat cross: A, National (susceptible); B, White Tartar (resistant)

TABLE 6.—*Breeding behavior for rust reaction of 86 F_3 families of oats grown from seed of individual F_2 plants of crosses between White Tartar and National (278a)*

Ratio	Breeding behavior in the F_3						
	Number of homozygous resistant		Number of heterozygous			Number of homozygous resistant	
	Families	Plants	Families	Plants		Families	Plants
				Resistant	Susceptible		
Observed	20.0	478	47	854	303	19.0	465
Calculated	21.5	478	43	868	289	21.5	465
Deviation	1.5	----------	4	14	14	2.5	----------

Assuming a 3:1 ratio, the 86 F_2 plants should have segregated in a ratio of 21.5 homozygous resistant to 43 heterozygous to 21.5 homozygous susceptible families. (Table 6.) The deviation of the calculated from the observed data needs no further comment.

Progenies of 83 plants of the F_3 were studied in the F_4 generation. All plants selected from homozygous resistant and homozygous susceptible F_3 rows bred true for resistance or susceptibility, respectively. Both resistant and susceptible F_3 plants were selected from the heterozygous F_3 rows and their progeny carried through the F_4 generation. These susceptible F_3 plants bred true for susceptibility, whereas two-thirds of the resistant plants segregated in a ratio of three resistant plants to one susceptible, and the other third bred true for resistance.

WHITE TARTAR×LINCOLN

The 175 F_2 plants of the cross White Tartar×Lincoln (253a) were sent to Ames from Ithaca and have the same history as the White Tartar×National. Lincoln is susceptible to stem rust while White Tartar is resistant. (Fig. 5.) From these F_2 individuals 4,405 plants were grown in the F_3. Of the F_3 families, 38, containing 948 plants, were homozygous for susceptibility; 44, containing 1,094 plants, were homozygous for rust resistance; 93, containing 2,363 plants, segregated in a ratio of 1,828 resistant plants to 535 susceptible plants.

Placing these results on a factorial basis, White Tartar could be expressed as *SSii* and Lincoln as *ssii*, where S = resistant and s = susceptible. A ratio of 3 resistant plants to 1 susceptible would be expected in the F_2. Assuming a 3:1 ratio, the deviation between the calculated and observed data is small. (Table 7.)

TABLE 7.—*Breeding behavior for rust reaction of 175 F_3 families of oats grown from seed of individual F_2 plants of crosses between White Tartar and Lincoln (253a)*

Ratio	Breeding behavior in the F_3						
	Number of homozygous resistant		Number of heterozygous			Number of homozygous susceptible	
			Families	Plants			
	Families	Plants		Resistant	Susceptible	Families	Plants
Observed	44.0	1,094	93.0	1,828	535	38.0	948
Calculated	43.7	1,094	86.5	1,773	590	43.7	948
Deviation	.3		6.5	55	55	5.7	

In 1922, 101 F_3 plants were studied for their reaction to rust in the F_4 generation. Of these 101 plants, 26, selected from a homozygous resistant F_3 progeny produced 342 F_4 plants, all of which were resistant. Eight susceptible F_3 plants, selected from homozygous susceptible F_3 progenies, bred true for susceptibility in the F_4 generation by producing 107 susceptible plants to none that was resistant.

Theoretically, there should have been three different kinds of plants in the heterozygous F_3, namely, two kinds of resistant and one susceptible. From the segregating F_3 families 43 resistant plants

FIG. 5.—Characteristic appearance of susceptible and resistant parents in an oat cross: A, Lincoln (susceptible); B, White Tartar (resistant).

were selected. Of this number, 12 bred true for resistance, producing 177 plants, and 31 segregated in the ratio of 313 resistant to 111 susceptible. The PE here, assuming the 3:1 ratio characteristic of a monohybrid, is ± 6.01 and the $\frac{D}{PE}$ is 0.831. Of the susceptible plants selected from the F_3, 24 bred true for susceptibility in the F_4, producing 291 plants. These F_4 families conform to expectation.

CROSSES OF RESISTANT VARIETIES

Rust Reaction of the F_2 and F_3 Plants

In order to study further the inheritance of resistance to stem rust, crosses were made between the two resistant varieties, Green Russian and Richland. As shown earlier (7), Richland possesses inherent resistance to stem rust. Additional crosses were made between White Russian and Ruakura. The latter parent was resistant, but less so than White Russian.

GREEN RUSSIAN×RICHLAND

The F_1 plants of the cross between Green Russian and Richland were more resistant than either parent. In fact, only a few small rust pustules were found. The F_2 plants, as shown in Table 8, segregated with many resistant plants and only a few susceptible ones. Here, again, the resistant plants were more resistant than either parent. The susceptible plants were severely attacked. Hybrid No. 277-4 produced 309 resistant plants to no susceptible ones in 1922, but the remnant seed of this cross produced 186 resistant and 3 susceptible plants in 1923.

Another cross of Green Russian×Richland (hybrid No. 277-3) was studied in the F_3 in 1922 and in 1923. The one susceptible F_2 plant produced 13 susceptible plants in 1922 and 99 susceptible plants in 1923. The 1,000 F_4 plants obtained from the 1922 F_3 susceptible plants all bred true for susceptibility in 1923. In 1922, the progenies of 333 resistant F_2 plants segregated into 244 which bred true for resistance to 89 which segregated. As only 20 seeds from each F_2 plant were sown for the F_3 population, it is probable that 244 resistant plants to 89 susceptible do not express the true ratio.

Table 8.—*Reaction to Puccinia graminis avenae of the F_1 and the F_2 plants from crosses between two resistant varieties of oats, Green Russian and Richland*

Hybrid No.	F_1 reaction	Number and reaction of F_2 plants	
		Resistant	Susceptible
277-1	Resistant	322	0
277-2	do	346	0
277-3	do	265	1
277-4 (1922)	do	309	0
277-4 (1923)	do	186	3
277-5	do	256	0

The possibility of a mechanical mixture as an explanation of the behavior of this cross is eliminated by the fact that distinct segrega-

tion for height of plant as well as color of the lemma occurred. In addition, the resistant hybrids possessed a more marked resistance than either parent, and the susceptible hybrids were intermediate between the two parents in height of plant.

WHITE RUSSIAN×RUAKURA

Both White Russian and Ruakura were classified as resistant, but the latter consistently showed more stem rust. All of the F_1 plants of the four families carried through the F_2 were resistant, as shown in Table 9. The crosses of these parents responded similarly to those of Green Russian × Richland.

TABLE 9.—*Reaction to Puccinia graminis avenae of the F_1 and F_2 plants from crosses between two resistant varieties of oats, White Russian and Ruakura*

Hybrid No.	F_1 reaction	Number and reaction of F_2 plants	
		Resistant	Susceptible
271–1	Resistant	245	1
271–2	do	100	0
271–3	do	335	5
271–4	do	154	0
Total		834	6

A total of 834 resistant to 6 susceptible plants was produced by all four families. Without doubt the White Russian × Ruakura crosses were hybrids, as evidenced by the typical monohybrid segregation for shape of panicle in the F_2 generation and also by the segregation for height of plant.

No attempt was made to give a factorial explanation of the results obtained by crossing resistant on resistant varieties, as it is probable that insufficient numbers were obtained to express the true ratios in the F_3. It is probable, however, that factors in addition to those considered in this paper are involved in the inheritance of rust resistance in the Green Russian × Richland and the White Russian × Ruakura crosses.

SUMMARY

Out of 770 pollinations, no hybrids were obtained from pollinations made between 11.30 o'clock a. m. and 2.30 o'clock p. m. under field conditions in central Iowa and northern Wisconsin. Pollination at the time of emasculation resulted in some selfed seeds, whereas pollination 24 to 72 hours after emasculation produced true hybrids and a percentage of fertility higher than that resulting after longer periods. Dusting the stigma with pollen produced a percentage of hybrids higher than by inserting the whole anther between the lemma and palea.

Marked hybrid vigor as expressed by yield was obtained in the F_1 generation of oat crosses.

Large uredinia were directly correlated with susceptibility to *Puccinia graminis avenae*.

Resistance to *P. graminis avenae* is dominant and due to a single-factor difference in White Tartar × National and White Tartar × Lincoln crosses.

At least three genetically different strains of Burt were found to breed true for susceptibility. One of these carried a factor which was an inhibitor of resistance. In a Burt × White Russian cross, the F_1 generation was susceptible, the F_2 segregated in the ratio of 3 resistant to 13 susceptible plants. In the F_3, these resistant F_2 plants produced 1 homozygous resistant progeny to 2 progenies which segregated in the proportion of 3 resistant plants to 1 susceptible. In another White Russian × Burt cross the F_1 generation was resistant and the F_2 generation segregated in the ratio of 3 resistant plants to 1 susceptible plant. In still another White Russian × Burt cross, the F_1 generation was susceptible and the F_2 segregated in the proportion of 1 resistant to 3 susceptible plants.

In crosses between resistant varieties such as Green Russian × Richland and White Russian × Ruakura, the F_1 plants were resistant. The F_2 segregated and produced some plants which were more resistant than either parent. It is probable that other factors than the two considered here are involved in the inheritance of resistance to *Puccinia graminis avenae.*

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